Kinetic Studies of Rabbit Muscle Lactate Dehydrogenase*

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A number of reports have appeared in recent years on the mechanism, i.e. the mode of enzyme and substrate interaction, of anaerobic dehydrogenases. For example, the mechanisms of heart muscle lactate dehydrogenase (1), yeast alcohol dehydrogenase (2), and ribitol dehydrogenase (3) appear to involve a compulsory sequence of enzyme and substrate interaction leading to one or more kinetically important ternary complexes. In 1951 Theorell and Chance (4) formulated a reaction sequence for liver alcohol dehydrogenase which involves only binary complexes; however, more recent studies indicate that whereas ternary complexes may be formed in the liver alcohol dehydrogenase reaction, they are short-lived relative to the binary complexes involving enzyme and coenzyme (5, 6).

Di- and triphosphopyridine nucleotide-linked dehydrogenase enzymes lend themselves conveniently to kinetic studies, as the concentration of reduced coenzyme can be measured simply and precisely. In most investigations, however, a number of mechanisms were found to be compatible with dehydrogenase kinetic data (7). In such instances it was necessary to correlate the dissociation constants determined kinetically with such constants evaluated by other means (8, 9). These latter analyses require a homogeneous preparation of enzyme of known molecular weight. In studying reversible reactions kinetically, it has proven advantageous to employ the Haldane relationship as suggested by Alberty (10). This method was recently utilized to exclude the "Theorell-Chance" mechanism (4) in the case of ribitol dehydrogenase (11). It was observed that there was a 50% discrepancy between the apparent equilibrium constant and this constant determined kinetically, and for this reason, the binary complex mechanism was omitted from consideration for ribitol dehydrogenase. Subsequent experiments, in which a different approach was used, appeared to establish the correctness of this view (3).

On the other hand, Theorell, Nygaard, and Bonnischen (5) reported good agreement between the Haldane equation for the binary complex mechanism and poor correlation between this equation and the ternary complex pathway of enzyme and substrate interaction.

The usefulness of studying reaction mechanisms in the absence and presence of product has very recently been suggested (3, 19). The steady state equations put forth to account for product inhibition include the possible formation of enzyme-reduced coenzyme-reduced product and enzyme-oxidized product (3). In seeking direct evidence for the existence of such compounds, it was observed that rabbit muscle lactate dehydrogenase, diphosphopyridine nucleotide, and pyruvate form a spectrophotometrically discernible compound which was thought to be enzyme-diphosphopyridine nucleotide-pyruvate (13). Other investigators have reported the probable existence of analogous reduced ternary complexes (14, 15).

The purpose of the present paper is to present data from kinetic studies which establish the mechanism of the lactate dehydrogenase system. It will be shown in this report that the dehydrogenase from rabbit muscle exhibits a mechanism similar to that suggested for liver alcohol dehydrogenase. Furthermore, additional support will be presented on the validity of studying reactions kinetically in the presence of product.

**EXPERIMENTAL PROCEDURE**

**Materials**—Lactate dehydrogenase from rabbit muscle was prepared by the method of Racker (16) and recrystallized three times according to the suggestion of Kornberg (17). DPN and DPNH were products of the Sigma Chemical Company. Sodium pyruvate and calcium l-lactate were obtained from the California Corporation for Biochemical Research. D L-Lactic acid was purchased from the Mallinckrodt Chemical Works and depolymerized by heating (1).

**Determinations**—Sodium pyruvate was assayed with excess DPNH and lactate dehydrogenase at pH 6.8. Pyruvate was calculated from the disappearance of DPNH by using 0.22 \times 10^3 \text{M}^{-1} \text{cm}^{-1} as the \text{mM} for the nucleotide (18). The sodium pyruvate used in the studies to be described was calculated to be 95.5% pure on a weight basis. Standard l-lactic acid was obtained by incubating a known amount of pyruvate with excess DPNH and lactate dehydrogenase until the absorbancy at 340 nm remained constant. This enzymatically prepared lactate was used as a standard for the colorimetric determination of DL-lactate and calcium l-lactate. The former compound was assayed by titration and found to be 90% pure when compared with the standard l-lactate by colorimetric analysis (19). Calcium l-lactate was found to be 77.8% pure on a weight basis when enzymatically prepared l-lactate was used as a standard for the colorimetric determination. Calcium l-lactate was converted to the acid with Dowex 50-H⁺ (20).

**Kinetic Studies**—Kinetic studies were carried out by measuring initial reaction velocities for various reaction mixtures spectrophotometrically. A Bausch and Lomb Spectronic 500 spectrophotometer was used to measure absorbancy changes. A coil of 3-inch copper tubing through which water at 28° was circulated was placed beside and below the cuvette holders of the...
instrument's cell compartment. Samples for analysis were prepared by adding appropriate amounts of substrates to 3.0 ml of 0.25 M phosphate buffer, pH 6.8, and diluting to 10 ml with distilled water that had been passed through an Amberlite MB-3 column (Rohm and Haas Company). The samples were maintained in a water bath at 28°C until assayed. The reactions were initiated with enzyme which had been diluted with ice-cold water immediately before each set of experiments and maintained in a Dewar flask at 3°C. Plasma albumin (Armour and Company) was added to the enzyme solution to give a final albumin concentration of 1 mg per ml. Absorbancy readings were taken at 340 nm for a period of 12 minutes. In the case of the forward reaction in which DPNH was produced, the solution in which the reaction occurred was read against a blank in which water had been substituted for enzyme. For the reverse reaction studies, velocity was recorded as the disappearance of DPNH.

A concentration of enzyme was chosen for each direction such that DPNH formation or loss was essentially linear for a period of from 8 to 12 minutes. Initial reaction velocities were recorded from the changes in DPNH absorbancy for the initial 10-minute period of the reaction. In cases when the velocity deviated from linearity at approximately 8 minutes, the initial reaction velocity during this time interval was extrapolated to 10 minutes.

All velocity measurements were corrected to a constant amount of enzymatic activity. Absorbancy readings were made in cylindrical cells of 5.0-cm light path.

RESULTS

It has been suggested by Alberty (7) that conclusions regarding possible mechanisms for two substrate systems may be made from kinetic studies in which one substrate is varied while the second is held constant at various levels. When such experiments are conducted at concentrations approximating the Michaelis constant for each substrate, certain insight into the possible reaction mechanism may be obtained by inspection of Lineweaver-Burk (21) type graphs. For those reaction mechanisms involving two substrate systems in which both substrates interact with enzyme before dissociation of either product, the following general rate equation should be obeyed (7):  

\[ v = \frac{V_I}{1 + \frac{K_A}{A} + \frac{K_B}{B} + \frac{K_{AB}}{A \cdot B}} \]  

By comparing the various kinetic parameters shown in Equation 1 and the analogous constants for the reverse reaction with the experimentally determined apparent equilibrium constant, it is possible to reduce the number of mechanisms that are described by Equation 1.

Endogenous substrate activity appeared to be absent when either substrate for the forward or reverse reaction was tested alone with lactate dehydrogenase. It was observed that inhibition occurred at elevated DPNH and pyruvate levels relative to those used in the experiments to be described. The concentration of substrates that could be used for kinetic experiments thus placed a restriction on the data obtained. In certain cases it was necessary to choose substrate concentrations that allowed for the production of relatively small amounts of product. The kinetic experiments were therefore carried out in 5-cm cylindrical cells in an attempt to circumvent these technical difficulties.

In Fig. 1 are presented double reciprocal-type plots for a series of experiments in the forward direction for the lactate dehydrogenase system in which L-lactate was varied at various concentrations of DPN. The lactate concentrations were held constant at 2.03 × 10^{-3} M ( ), 1.17 × 10^{-2} M ( ), 0.84 × 10^{-3} M ( ), and 0.59 × 10^{-3} M ( ); v was determined as a function of L-lactate concentration, which was varied in the range from 1.44 × 10^{-2} M to 2.4 × 10^{-3} M. Velocities are expressed as the molar concentration of DPNH formed in the reaction mixture over a period of 10 minutes after addition of enzyme. Other experimental details are given under "Experimental Procedure."
The kinetics of lactate dehydrogenase.

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It is apparent from the data presented in Figs. 1 to 4 that all of the Lineweaver-Burk plots have certain common characteristics; i.e. they are all linear and have a point of common intercept to the left of the 1/v axis. Furthermore, the ordinates of the points of common intercept are identical for the two studies of the forward reaction; in the case of the reverse reaction, the same is true. From the agreement of these experimental data with Equation 1, a number of possible mechanisms for lactate dehydrogenase were eliminated from consideration; however, as shown by Alberty (7), three types of reaction mechanisms might be expected to yield data compatible with those shown in Figs. 1 to 4. They are (a) a compulsory binding sequence of substrates and enzyme involving two binary complexes; (b) a compulsory pathway leading to the formation of one or more kinetically indistinguishable ternary complexes; and (c) a random order of enzyme-substrate binding leading to the formation of two kinetically significant ternary complexes in which the equilibria are adjusted rapidly except for the interconversion of the ternary complexes.

Secondary plots (22) of the data shown in Figs. 1 to 4 for the forward and reverse reactions are shown in Figs. 5 and 6, respectively. These graphs of reciprocal apparent maximal velocity versus reciprocal substrate concentration along with the data in Figs. 1 to 4 were used to evaluate the kinetic parameters shown in Table I. The linearity of the curves in Figs. 5 and 6 and the convergence of the lines at a common point on the y axis appear to confirm the accuracy of the aforementioned kinetic experiments.

In studying the kinetics of the forward reaction it was observed that the d isomer of lactic acid acts neither as a substrate nor as an inhibitor of rabbit muscle lactate dehydrogenase. A similar conclusion regarding the enzyme from heart muscle was reached by other investigators (1, 24, 25). The experiments presented in these studies were conducted first with L-lactate and reverse reaction. The experimental protocols are presented in the legends to the respective figures.
were subsequently repeated with the racemic mixture. The data obtained with the DL mixture and with the L isomer alone were essentially identical.

Albert (7) has described in detail the value of correlating the apparent equilibrium constant determined experimentally with kinetic parameters obtained for enzymatically catalyzed reactions of the type, \( A + B \rightarrow C + D \). In the case of rabbit muscle lactate dehydrogenase,

\[
K_{app} = \frac{[DPNH](pyruvate)}{[DPN](l-lactate)}
\]

Hakala, Ghad, and Schwert (1) have studied the effect of temperature on the apparent equilibrium constant, and by using their data a value at \( 25^\circ \text{C} \) of \( 2.19 \times 10^{-4} \) was obtained from a van't Hoff plot. According to the Haldane relationship, for mechanisms consistent with the data in Figs. 1 to 6, the following relationship should prevail (7).

\[
K_{app} = \frac{V_iK_{DPNH-pyruvate}}{V_iK_{DPNH-L-lactate}}
\]

A value of \( 4.80 \times 10^{-4} \) was calculated with this equation and the data presented in Table I.

For reactions in which the “Theorell-Chance” or binary complex mechanism is applicable, the apparent equilibrium constant and the kinetic parameters of the system are related by the following equation (7).

\[
K_{app} = \frac{V_iK_{DPNH-pyruvate}}{V_iK_{DPNH-L-lactate}}
\]

It was found for the rabbit muscle enzyme, however, that a value of \( 1.10 \times 10^{-4} \) was obtained with this equation and the kinetic parameters of Table I. Considering the discrepancy between the calculated values of \( 4.85 \times 10^{-4} \) from Equation 2 and \( 1.10 \times 10^{-4} \) from Equation 3 relative to the apparent equilibrium constant for the lactate dehydrogenase reaction, it was felt that the Haldane relationship could not be employed either to exclude or to substantiate the “Theorell-Chance” mechanism. Obviously, the data of Figs. 1 to 6 are not exact enough to permit such a choice of mechanism to be made. Thus, the kinetic data appear to be in harmony with all three mechanisms described above which are consistent with Equation 1.

**Product Inhibition Studies** — It has recently been suggested that a choice of mechanism could be made from kinetic studies alone for systems governed by rate laws of the type shown in Equation 1 (3, 12). By using this approach, which involves steady state kinetic type experiments conducted in the absence and presence of product, it should be possible to arrive at a definitive conclusion regarding the mechanism of rabbit muscle lactate dehydrogenase. Furthermore, such experiments permit one to make a decision regarding the identity of the substrate which reacts with the enzyme first in the case of compulsory-type mechanisms. A more complete treatment of this kinetic approach is presented elsewhere (3, 12).

If one were to assume the following mechanism for lactate dehydrogenase,

\[
E + DPN \xrightarrow{k_1} E-DPN
\]

\[
E-DPN + L-lactate \xrightarrow{k_2} E-DPNH + pyruvate
\]

\[
E-DPNH \xrightarrow{k_3} E + DPN H
\]

the steady state rate equation for the forward reaction is (23)

\[
\frac{E_0}{v} = \frac{1}{k_8} + \frac{1}{k_8(A)} + \frac{1}{k_8(B)} + \frac{k_9}{k_8k_9(A)(B)}
\]

where \( E_0, A, \) and \( B \) represent total enzyme concentration, DPN, and L-lactate, respectively.

If DPNH is present initially with substrates for the forward reaction, it is thought to have two kinetically significant effects (3, 12). First, it may compete with DPN for free enzyme \( E \), and, second, the complex, \( E-DPNH \), may form an abortive ternary complex with L-lactate of the type, \( E-DPNH-L-lactate \). To account for the effect of DPNH, Equation 7 is modified as follows (3).

\[
\frac{E_0}{v} = \frac{1}{k_8} + \frac{1}{k_8(A)} + \frac{1}{k_8(B)} + \frac{k_9}{k_8k_9(A)(B)}
\]

where \( C \) represents DPNH, and \( K_i \), the dissociation constant of the enzyme-DPNH-L-lactate complex.

When kinetic experiments are performed in the presence of the product of the second substrate, i.e., pyruvate, there occurs an alteration in the rate law shown in Equation 7. Pyruvate should cause a reversal of the reaction in which it is produced from the steady state rate equation for the forward reaction is (23)

\[
\frac{E_0}{v} = \frac{1}{k_8} + \frac{1}{k_8(A)} + \frac{1}{k_8(B)} + \frac{k_9}{k_8k_9(A)(B)}
\]

where \( D \) and \( K_{di} \) represent pyruvate and the dissociation constant of the enzyme-DPNH-L-lactate complex.

* For the reverse reaction, \( K_i \) is replaced by \( K_{di} \), the dissociation constant of the enzyme-DPNH-pyruvate complex.

### Table I

<table>
<thead>
<tr>
<th>Kinetic parameters of lactate dehydrogenase system calculated by methods of Florini and Vestling (22) and Dalziel (23)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( V_i )</td>
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<tr>
<td>( K_{DPNH} )</td>
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<tr>
<td>( K_{l-lactate} )</td>
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<tr>
<td>( K_{DPNH-L-lactate} )</td>
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<tr>
<td>( V_f )</td>
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<tr>
<td>( K_{DPNH} )</td>
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<tr>
<td>( K_{pyruvate} )</td>
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<td>( K_{DPNH-pyruvate} )</td>
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* \( E_0 \) represents total enzyme concentration (M). It is not possible to determine the absolute values for the rate constants without a knowledge of \( E_0 \).
Fig. 7. Plot of reciprocal of initial reaction velocity (v) versus reciprocal of molar concentration of L-lactate. The concentrations of pyruvate are: X, none; ■, 3.05 × 10^-4 M; □, 5.07 × 10^-4 M; ●, 6.1 × 10^-4 M; ○, 7.65 × 10^-4 M. DPN concentration was maintained at a constant level of 1.46 × 10^-3 M, and lactate varied in the range from 6.70 × 10^-3 M to 1.44 × 10^-2 M. v is expressed as in Fig. 1. Other experimental details are given under “Experimental Procedure.” The K_i values calculated from Equation 9 are 1.40 × 10^-4 M, 1.68 × 10^-4 M, 1.75 × 10^-4 M, and 1.55 × 10^-4 M at pyruvate concentrations of 3.05 × 10^-4 M, 5.07 × 10^-4 M, 6.1 × 10^-4 M, and 7.65 × 10^-4 M, respectively.

Fig. 8. Plot of reciprocal of initial reaction velocity (v) versus reciprocal of molar concentration of DPN. The concentrations of pyruvate are: ■, none; □, 2.78 × 10^-3 M; ●, 5.58 × 10^-3 M; ○, 7.2 × 10^-3 M. L-Lactate concentration was held constant at 1.20 × 10^-2 M, and DPN varied in the range from 1.82 × 10^-3 M to 7.18 × 10^-4 M. v is expressed as in Fig. 1. Other experimental details are given under “Experimental Procedure.” The K_i values calculated from Equation 9 are 0.976 × 10^-4 M, 0.992 × 10^-4 M, and 0.935 × 10^-4 M at pyruvate concentrations of 2.78 × 10^-3 M, 5.58 × 10^-3 M, and 7.2 × 10^-3 M, respectively.

Fig. 9. Plot of reciprocal of initial reaction velocity (v) versus reciprocal of molar concentration of pyruvate. The concentrations of L-lactate are: ■, none; □, 2.4 × 10^-2 M; ●, 4.0 × 10^-2 M; ○, 7.2 × 10^-2 M. DPNH was held constant at 4.24 × 10^-6 M, and pyruvate varied in the range from 7.35 × 10^-4 M to 1.38 × 10^-3 M. v is expressed as in Fig. 3. Other experimental details are given under “Experimental Procedure.” The K_i values calculated from Equation 9 are 0.384 M, 0.381 M, and 0.590 M at L-lactate concentrations of 2.4 × 10^-2 M, 4.0 × 10^-2 M, and 7.2 × 10^-2 M, respectively.

Fig. 10. Plot of reciprocal of initial reaction velocity (v) versus reciprocal of molar concentration of DPNH. The concentrations of L-lactate are: ■, none; □, 2.72 × 10^-3 M; ●, 5.4 × 10^-3 M; ○, 7.2 × 10^-3 M. Pyruvate was held constant at 4.60 × 10^-4 M, and DPNH varied in the range from 4.55 × 10^-6 M to 1.30 × 10^-5 M. v is expressed as in Fig. 3. Other experimental details are given under “Experimental Procedure.” The K_i values calculated from Equation 9 are 0.198 M, 0.172 M, and 0.272 M at L-lactate concentrations of 2.72 × 10^-2 M, 5.4 × 10^-2 M, and 7.2 × 10^-2 M, respectively.

It had been reported previously that insight into reaction mechanisms of the type consistent with the experimental data already presented for lactate dehydrogenase can be obtained from studies in which the effect of the product of the second substrate is considered (3).

For the reverse reaction, K_i is replaced by K_i, the dissociation constant of the enzyme-DPNH-L-lactate complex.
yield a decrease in apparent maximal velocity in the presence of sugar product (3). Actually the sugar product, as predicted by Equation 9, causes an increase in apparent Michaelis constant with no alteration in maximal velocity. When the random ternary complex sequence is considered (3), it can be noted that although the data of Figs. 7 and 9 agree well with this binding pathway, the data in Figs. 8 and 10 are at variance with this mechanism. In the legends to Figs. 7 to 10 are shown the calculated dissociation constants \( K_i \) and \( K_{ii} \) for the abortive ternary complexes thought to be produced if the "Theorell-Chance" mechanism (4) is applicable to rabbit muscle lactate dehydrogenase. These values were obtained by using the various rate constants shown in Table I and the data in the respective figures.

From the foregoing discussion, it appears that the coenzyme substrates add to the enzyme before the addition of sugar substrates.

The data described in Figs. 11 to 14 were obtained from kinetic experiments carried out with and without coenzyme product for the forward and reverse reaction. These data are consistent with all three mechanisms that are possible for systems governed by Equation 1. From plots of this type, it is possible to suggest that the sequence of substrate interaction with enzyme involves coenzyme addition first and sugar substrate second, regardless of the actual mechanism, except in the case of the random binding pathway (3). In the legends to Figs. 11 and 13 are shown the calculated dissociation constants for the oxidized and reduced abortive ternary complexes. These values were obtained from the rate constants presented in Table I, the data in Figs. 11 and 13, and Equation 8. In Figs. 12 and 14 are shown experimental data obtained for both the forward and reverse reactions in the presence or absence of coenzyme product. The lines shown on the graphs were "theoretical" curves which were drawn by using Equation 8. It can be seen that these curves agree well with the data obtained experimentally.

**DISCUSSION**

The kinetic data presented in this report for the rabbit muscle lactate dehydrogenase system are consistent with a compulsory
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sequence of substrate binding to the enzyme involving kinetically significant binary complexes. The coenzyme substrates, as might be expected from studies of other dehydrogenases (1–4), react with the enzyme before the addition of L-lactate and pyruvate. Most of the definitive conclusions alluded to regarding the reaction mechanism of the dehydrogenase were obtained from investigations of product inhibition. Recently Fromm and Nelson (3) partially elucidated the mechanism for ribitol dehydrogenase from kinetic experiments of a type similar to those described in the present paper. Unfortunately, these investigators studied the kinetics of the ribitol enzyme quantitatively in only one direction. In the present investigation, product inhibition studies of both the forward and reverse reactions were undertaken. A comparison of the dissociation constants, \( K_i \) and \( K_{ii} \), for the abortive ternary complexes, E-DPNH-L-lactate and E-DPN-pyruvate, obtained from separate experimental kinetic determinations revealed fairly good agreement among the calculated values. The average value of the dissociation constant for the E-DPNH-L-lactate complex was 0.209 \( \mu \)m, whereas that obtained for the oxidized complex, E-DPN-pyruvate, was 2.02 \( \times \) \( 10^{-4} \) \( \mu \)m.

The present report lends additional credence to the original suggestions regarding the usefulness of studying reaction mechanisms kinetically in the presence and absence of products (3). It is obvious from these investigations that partial elucidation of enzymatic reaction mechanisms can be attained with enzyme preparations purified only to the point needed for conventional kinetic experiments. Although a homogeneous enzyme preparation is obviously highly desirable, it is not a requisite for studies of the type outlined in the present report.

From the data presented above, it seems probable that pyruvate and L-lactate occupy the same enzymatic locus. In the derivation of Equations 8 and 9, it was assumed that these compounds act as competitive inhibitors (3). Similar assumptions regarding coenzyme substrates and products were advanced by Alberty (12). Thus, with respect to ribitol and lactate dehydrogenase from rabbit muscle it appears that the suggestion of Krukpa and Laidler (26) relative to separate binding sites for the sugar substrates is untenable. If this latter hypothesis were valid for the two aforementioned dehydrogenases, the equations derived to account for competitive inhibition between the second substrate and its product would not be expected to agree with the experimental results presented above. Novoa et al. (27) have also suggested that the conclusions of Krukpa and Laidler (26) may not be valid.

It might be well to mention that Winer and Theorell (28) reported ternary complexes of a type analogous to those reported here for liver alcohol dehydrogenase. These complexes were of the enzyme-coenzyme-competitive substrate inhibitor type. Obviously, for binary complex mechanisms of the "Theorell-Chance" variety (4), intermediate ternary complexes do occur; however, they are not kinetically important relative to the coenzyme binary complexes (5–7).

SUMMARY

The mechanism of the lactate dehydrogenase enzyme system from rabbit skeletal muscle was investigated kinetically by employing the approach of product inhibition. On the basis of kinetic data obtained, it appears that the mechanism of the reaction involves a compulsory sequence of substrate binding to enzyme with the formation of kinetically significant binary complexes. Pyruvate and L-lactate probably occupy the same enzymatic site. Similarly, the coenzyme substrates and products occupy a common enzymatic locus which differs from that of the acid substrates. Dissociation constants for the abortive ternary complexes, enzyme-reduced diphosphopyridine nucleotide-L-lactate and enzyme-diphosphopyridine nucleotide-pyruvate, were calculated from equations previously derived. These complexes are formed when product is included initially with substrates.

The usefulness of product inhibition studies conducted in the presence of both coenzyme and acid products is discussed.

Addendum—Fawcett, Ciotti, and Kaplan (29) have recently reported that repeated freezing and thawing of DPNH solutions result in conversion of the nucleotide to an inhibitory compound. DPNH solutions used for studies of lactate dehydrogenase reported above were prepared every 2 or 3 days. In light of the observations of Fawcett, Ciotti, and Kaplan (29), all experiments in which DPNH was used either as a substrate or product were repeated with fresh solutions prepared with the commercial solid compound immediately before each kinetic experiment. The results obtained from these experiments were essentially the same as those reported in the present paper.

REFERENCES

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